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Abundance, species composition and phenology of Pauropoda (Myriapoda) from a secondary upland forest in Central Amazonia

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Abundance, species composition and phenology of Pauropoda (Myriapoda) from a secondary upland forest in Central Amazonia. - The 6,878 pauropods collected within 12 months in the soil (0-7 cm depth) of a secondary upland forest (1,085.7 ± 42.3 ind./m^2/month) near Manaus were represented by 41 species of the Pauropodidae (Order Tetramerocerata). The Pauropodinae were represented by 31 species, the Polypauropodinae by 6 species, and the Scleropauropodinae by 4 species. About half of all pauropod specimens obtained inhabited the organic soil layer (0-3.5 cm depth) compared to the mineral subsoil (3.5-7 cm). Abundance of pauropods in the soil was twice as high in comparison to the Symphyla from the same study site. The lack of a distinct reproductive period in eudominant and dominant pauropod species and the presence of juveniles and adults throughout the year indicate a plurivoltine mode of life. Only in one species was the monthly catch of adults positively correlated with maximum temperatures of the soil. Pauropods obtained from the soil of four other upland forests in Central Amazonia (0-14 cm depth) accounted for 1.1-4.4% of the total soil arthropods. A possible parthenogenesis found in three pauropod species is discussed.

Key-words: abundance - phenology - parthenogenesis - soil fauna - Pauropoda - Amazon - Neotropics.

INTRODUCTION

Terrestrial arthropods of Central Amazonian forests have been investigated for several years (cf. ADIS & SCHUBART 1984; ADIS 1997; ADIS *et al.* 1997a,b) in a co-operative venture between the National Institute for Amazonian Research (INPA) at Manaus/Brazil and the Tropical Ecology Working Group at the Max-Planck-Institute for Limnology in Plön/Germany (Projeto INPA/Max-Planck). Data on abundance and

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phenology of Pauropoda sampled during 12 months in 1982/83 in a secondary upland forest are now available, as their taxonomical evaluation has been completed (SCHELLER 1994, 1997). Our data represent the very first contribution on the abundance and phenology of Neotropical pauropod species. Voucher specimens have been deposited at the Systematic Entomology Collections of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus/Brazil and at the Muséum d'histoire naturelle in Geneva/ Switzerland.

STUDY AREA, MATERIAL AND METHODS

Pauropods were collected between 1981 and 1983 in the course of ecological studies on Central Amazonian arthropods from a previously investigated and fully described secondary upland forest at Rio Tarumã Mirím (03°02'S, 60°17'W), a tributary of the Rio Negro near Manaus, where the vegetation was previously cut but unburned (cf. ADIS 1992, FRANKLIN *et al.* 1997). The forest is subject to a rainy season (December-May: average precipitation 1550 mm; 258.8 ± 36.8 mm/month) and a "dry" season (June-November: average precipitation 550 mm; 91.8 ± 43.8 mm/month, but each month with some rain events; cf. RIBEIRO & ADIS 1984). The yellow latosol (= ferrasol in JORDAN 1984) of the secondary upland forest supported a 2-3 cm thick humus layer, interspersed with fine roots, and a thin surface covering of leaf-litter. One ground photo-eclector (emergence trap with pitfall trap inside) and one arboreal photo-eclector for trunk ascents (funnel trap) were installed in the forest from December 1981 to December 1982 (see ADIS & SCHUBART 1984). The distribution of pauropods in the soil was studied between September 1982 and August 1983 (RODRIGUES 1986). Twelve soil samples were taken once a month every two meter along a randomly selected transect. The split corer composed of a steel cylinder with lateral hinges (diameter 21 cm, length 33 cm), was driven into the soil by a mallet. Each sample of 7 cm depth was then divided into two subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of Kempson (ADIS 1987). The combined area of 12 samples represented 0.42 m^2. Calculated average abundances per m^2 are given with sample standard deviation. The monthly collection data of pauropods from the two soil layers in relation to changing conditions of precipitation, temperature and humidity of the air near the forest floor as well as moisture content, temperature and pH of the soil were statistically evaluated with a linear, parametric correlation test (CAVALLI-SFORZA 1972) using the original field data (RODRIGUES 1986). Pauropoda (Pauropodidae) sampled were classified as juveniles (3, 5 and 6 pairs of legs), subadults (8 pairs of legs) and adults (9 pairs of legs). Sex was determined for subadults and adults.

RESULTS

A total of 6,878 pauropods (body length ≤1.50 mm without antennae) were collected. Out of these, 90% could be identified to species and developmental stages. All pauropods were obtained by extraction of the forest soil. None were caught on the soil surface (ground photo-eclector), or on the tree trunk (arboreal photo-eclector).

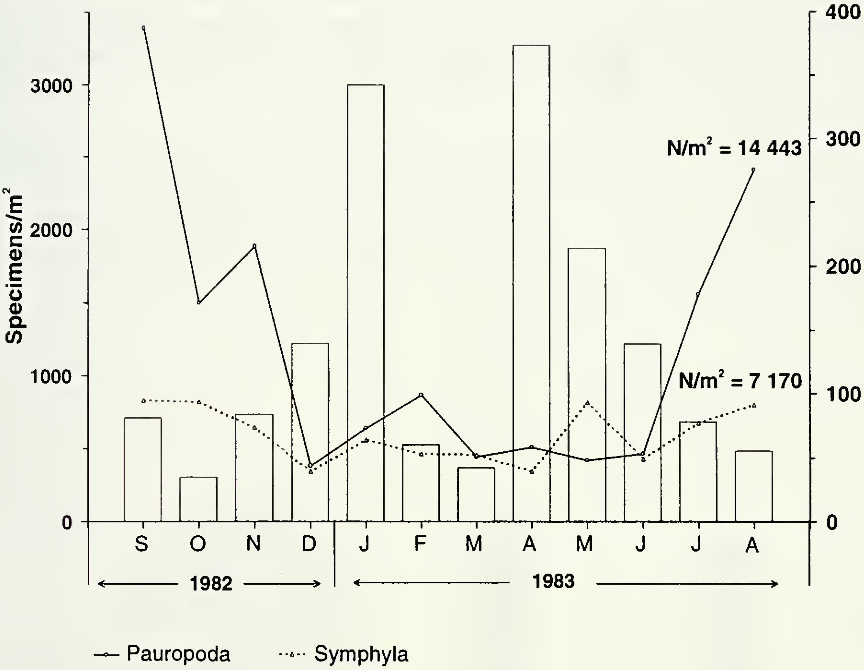

FIG. 1

Distribution of Pauropoda and Symphyla in the soil. Samples taken monthly at 0-7 cm depth between September 1982 and August 1983 in a secondary upland forest near Manaus. (N = total number of specimens). Total precipitation per month given between sampling dates (= in the middle of each month). The low rainfall observed in early 1983 was due to a strong El Niño-event (cf. ADIS & LATIF 1996).

TABLE 1

Average abundance (N/m^2) and dominance (%) of Pauropoda genera (all representing the Pauropodidae) in the soil of a secondary upland forests near Manaus, Brazil. Samples taken monthly at 0-3.5 and 3.5-7.0 cm soil depths between September 1982 and August 1983.

PAUROPODIDAE	N/m² per month			%
Genus (Species)	0 - 3.5 cm	3.5 - 7.0 cm	0 - 7.0 cm	0 - 7.0 cm
Allopauropus (28)	486.6 ± 24.8	509.1 ± 26.3	995.7 ± 49.6	91.7
Hemipauropus (2)	34.1 ± 6.6	16.4 ± 4.7	50.5 ± 10.4	4.7
Polypauropus (2)	17.3 ± 7.4	12.2 ± 6.0	29.5 ± 13.3	2.7
Scleropauropus (4)	2.0 ± 0.6	1.8 ± 0.7	3.8 ± 1.2	0.3
Polypauropoides (4)	1.4 ± 0.4	4.0 ± 0.9	5.4 ± 1.1	0.5
Cauvetauropus (1)	0.4 ± 0	0.4 ± 0	0.8 ± 0	0.1
Total	541.8 ± 21.1	543.9 ± 22.4	1085.7 ± 42.3	100.0

Pauropoda represented 6.4% of the total arthropods extracted from soil samples within 12 months (Acari & Collembola omitted; cf. RODRIGUES 1986). Their abundance in 0-7 cm soil depth was twice as high than that of the Symphyla (Fig. 1: 14,443 versus 7,170 ind./m^2; cf. ADIS *et al.* 1997c). An average abundance of 1,085.7 ± 42.3 pauropods/m^2/month was recorded in 0-7 cm soil depth (Table 1).

About half of the pauropods obtained (49.9%) inhabited the organic soil layer (Fig. 2: 0-3.5 cm) compared to the mineral subsoil (3.5-7.0 cm depth). Of the total catch, 68.8% was represented by adults (Fig. 2), 4.6% by subadults and 26.6% by juveniles. The total catch of pauropods collected during the dry season was three times higher compared to the rainy season: 77.5% (1,865.2 ± 980.5 ind./m^2/month) versus 22.5% (542.0 ± 180.2 ind./m^2/month).

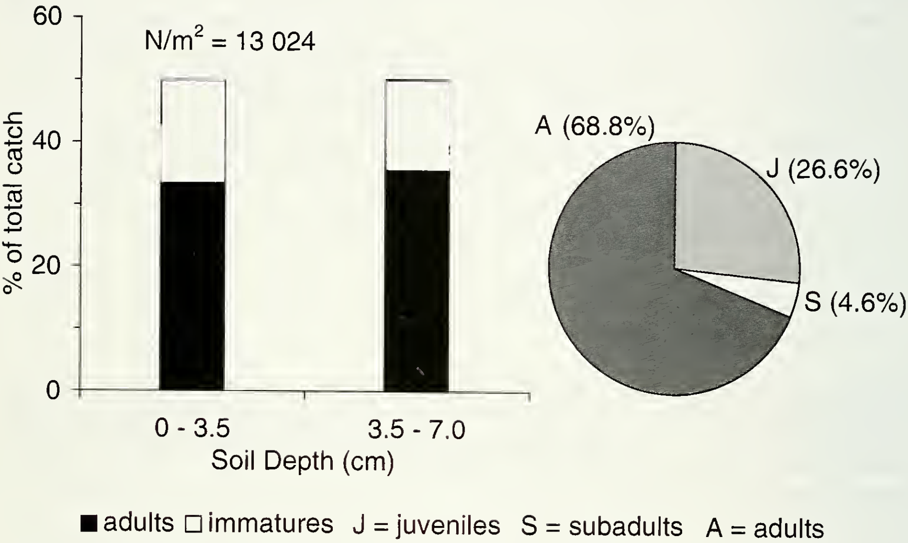

FIG. 2

Distribution of Pauropoda in the soil according to depth, and percentage of developmental stages in a secondary upland forest near Manaus. (Total catch = 100%). Samples taken monthly at 0-3.5 and 3.5-7 cm depths between September 1982 and August 1983. (N = total number of specimens).

The pauropods collected from the secondary upland forest represented 41 species of the family Pauropodidae (Order Tetramerocerata). Out of these, 38 were new (SCHELLER 1994, 1997) and only 3 known (Table 2). *Allopauropus*, *Hemipauropus* and *Cauvetauropus* represented the subfamily Pauropodinae (31 species), *Polypauropus* and *Polypauropoides* the subfamily Polypauropodinae (6 species), and *Scleropauropus* the subfamily Scleropauropodinae (4 species). Out of the six genera obtained (Tables 1, 2), *Allopauropus* (28 species) represented 91.7% of the total catch, *Hemipauropus* (2 species) 4.6%, and *Polypauropus* (6 species) 2.7%. Representatives of the genus *Allopauropus* were as abundant in the organic soil layer as in the mineral subsoil

TABLE 2

Average abundance (N/m^2) and dominance (%) of Pauropoda species (all representing the Pauropodidae) in the soil of a secondary upland forests near Manaus, Brazil. Samples taken monthly at 0-3.5 and 3.5-7.0 cm soil depths between September 1982 and August 1983.

	Species	Subf.	N/m^2 per month			%
No.			0 - 3.5 cm	3.5 - 7.0 cm	0 - 7.0 cm	0 - 7.0 cm
1	*Allopauropus* (A.) *rodriguesi Sch.*	Pau.	174.0 ± 233.3	184.1 ± 223.1	358.1 ± 441.2	33.0
2	*Allopauropus* (D.) *bicornutus* Sch.	Pau.	78.4 ± 94.9	126.9 ± 153.4	205.3 ± 238.7	18.9
3	*Allopauropus* (D.) *proximus* Remy	Pau.	48.3 ± 76.8	11.6 ± 14.1	59.9 ± 88.7	5.5
4	*Allopauropus* (A.) *dundoensis* Remy	Pau.	31.3 ± 49.5	22.1 ± 31.1	53.4 ± 79.1	4.9
5	*Allopauropus* (A.) *tenuis* Remy	Pau.	27.7 ± 35.7	22.6 ± 29.0	50.3 ± 63.6	4.6
6	*Allopauropus* (A.) *ovalis* Sch.	Pau.	22.9 ± 18.0	24.8 ± 22.3	47.7 ± 34.2	4.4
7	*Allopauropus* (D.) *manausensis* Sch.	Pau.	23.5 ± 17.0	23.1 ± 10.9	46.6 ± 29.0	4.3
8	*Allopauropus* (A.) *bicorniculus* Sch.	Pau.	10.6 ± 11.1	33.5 ± 24.4	44.1 ± 29.2	4.1
9	*Hemipauropus piriformis* Sch.	Pau.	24.3 ± 18.9	9.9 ± 11.9	34.2 ± 29.5	3.1
10	*Allopauropus* (D.) *adisi* Sch.	Pau.	15.4 ± 13.0	13.8 ± 9.4	29.2 ± 20.7	2.7
11	*Polypauropus tropicus* Sch.	Pol.	16.2 ± 23.1	12.0 ± 19.2	28.2 ± 41.7	2.6
12	*Allopauropus* (D.) *anomoios* Sch.	Pau.	9.1 ± 13.5	12.8 ± 14.6	21.9 ± 27.0	2.0
13	*Allopauropus* (D.) *ieenus* Sch.	Pau.	10.6 ± 12.7	7.2 ± 14.8	17.8 ± 25.7	1.6
14	*Hemipauropus amazonicus* Sch.	Pau.	9.9 ± 7.9	6.5 ± 10.7	16.4 ± 17.1	1.5
15	*Allopauropus* (D.) *brachypodus* Sch.	Pau.	6.4 ± 10.1	3.4 ± 6.0	9.8 ± 11.8	0.9
16	*Allopauropus* (A.) *uncinatus* Sch.	Pau.	4.8 ± 8.2	4.4 ± 7.2	9.2 ± 13.7	0.8
17	*Allopauropus* (D.) *petiolatus* Sch.	Pau.	3.6 ± 4.8	5.2 ± 10.1	8.8 ± 12.0	0.8
18	*Allopauropus* (D.) *irmgardae* Sch.	Pau.	3.2 ± 5.1	4.4 ± 5.8	7.6 ± 8.2	0.7
19	*Allopauropus* (D.) *pedicellus* Sch.	Pau.	5.6 ± 5.8	1.8 ± 2.7	7.4 ± 5.8	0.7
20	*Allopauropus* (D.) *junki* Sch.	Pau.	5.6 ± 7.9	1.0 ± 1.9	6.6 ± 8.9	0.6
21	*Allopauropus* (D.) *neotropicus* Sch.	Pau.	1.2 ± 2.2	2.6 ± 2.9	3.8 ± 4.6	0.4
22	*Allopauropus* (D.) *tohoius* Sch.	Pau.	1.8 ± 4.3	1.0 ± 2.2	2.8 ± 6.0	0.3
23	*Scleropauropus tarumamirimi* Sch.	Scl.	1.2 ± 0.4	1.6 ± 0.4	2.8 ± 5.1	0.3
24	*Allopauropus* (D.) *sinuosus* Sch.	Pau.	1.4 ± 2.9	0.4 ± 0.4	1.8 ± 3.6	0.2
25	*Polypauropoides biclaviger* Sch.	Pol.	0.6 ± 1.2	1.0 ± 2.4	1.6 ± 2.9	0.1
26	*Polypauropoides foliolus* Sch.	Pol.	0.6 ± 1.4	1.0 ± 2.2	1.6 ± 2.9	0.1
27	*Polypauropoides unisetus* Sch.	Pol.	-	1.6 ± 2.9	1.6 ± 2.9	0.1
28	*Allopauropus* (D.) *dischides* Sch.	Pau.	0.8 ± 1.7	0.6 ± 1.4	1.4 ± 2.4	0.1
29	*Polypauropus latebricolus* Sch.	Pol.	1.0 ± 2.2	0.2 ± 0.7	1.2 ± 2.2	0.1
30	*Cauvetauropus (P.) biglobulosus* Sch.	Pau.	0.4 ± 1.4	0.4 ± 1.0	0.8 ± 1.7	0.1
31	*Allopauropus* (D.) *acer* Sch.	Pau.	0.2 ± 0.7	0.6 ± 1.0	0.8 ± 1.4	0.1
32	*Polypauropoides naous* Sch.	Pol.	0.2 ± 0.7	0.4 ± 1.4	0.6 ± 2.2	0.1
33	*Allopauropus* (D.) *aius* Sch.	Pau.	-	0.4 ± 1.0	0.4 ± 1.0	>0.1
34	*Scleropauropus beritae* Sch.	Scl.	0.4 ± 1.4	-	0.4 ± 1.4	>0.1
35	*Scleropauropus rimatus* Sch.	Scl.	0.2 ± 0.7	0.2 ± 0.7	0.4 ± 1.4	>0.1
36	*Allopauropus* (D.) *campinaranicus* Sch.	Pau.	0.2 ± 0.7	-	0.2 ± 0.7	>0.1
37	*Allopauropus* (D.) *korynetes* Sch.	Pau.	-	0.2 ± 0.7	0.2 ± 0.7	>0.1
38	*Allopauropus* (D.) *hylaios* Sch.	Pau.	-	0.2 ± 0.7	0.2 ± 0.7	>0.1
39	*Allopauropus* (D.) *mirimus* Sch.	Pau.	-	0.2 ± 0.7	0.2 ± 0.7	>0.1
40	*Allopauropus* (D.) *tenuilobatus* Sch.	Pau.	-	0.2 ± 0.7	0.2 ± 0.7	>0.1
41	*Scleropauropus fissus* Sch.	Scl.	0.2 ± 0.7	-	0.2 ± 0.7	>0.1
	Total		541.8 ± 21.1	543.9 ± 22.4	1085.7 ± 42.3	100.0

Subf. = Subfamily, Pau. = Pauropodinae, Pol. = Polypauropodinae, Scl. = Scleropauropodinae

(48.9% versus 51.1%; Fig. 3: top; Table 1). Species representing the genus *Hemipauropus* (Fig. 3) were somewhat more abundant in the organic layer (0-3.5 cm: 67.5% of the total catch; Table 1), whereas representatives of the genus *Polypauropoides* (Table 1) were more abundant in the mineral subsoil (3.5-7 cm: 74.1%). Out of the total 41 pauropod species, 3 species were only obtained from the organic soil layer and 5 solely from the mineral subsoil (Table 3, Fig. 3: bottom). Three species of the genus *Allopaurus* represented more than half (57.4%) of the total pauropods collected in 0-7 cm soil depth, 27% in the organic soil layer (0-3.5cm) and 30% in the mineralic subsoil (3.5-7cm; Fig. 3: bottom, Table 1).

Allpauropus rodriguesi and *A. bicornutus* were eudominant, representing 33.0% (4,296 ind./m2) and 18.9% (2,460 ind./m^2) of the total catch, respectively (Fig. 4, Table 1). Adult specimens predominated in both species (61.9 and 83.3%, respectively), regardless of the soil layer investigated (Fig. 4), whereas subadults were rare (<2%). Juvenile specimens were more abundant in *A. rodriguesi* (37.3% of the total catch) compared to *A. bicornutus* (14.9%). *A. rodriguesi* was likewise abundant in both soil layers (Table 1, Fig. 4), despite its large body size (≤1.41mm) and relatively long legs. *A. bicornutus* was smaller (≤0.83mm) and somewhat more abundant in the mineral subsoil (3.5-7cm: 62% of the total catch) compared to the organic soil layer (0-3.5cm).

The next two dominant species, *A. proximus* and *A. dundoensis* (Fig. 4, Table 1), represented 5.5% (719 ind./m^2) and 4.9% (638 ind./m^2) of the total catch, respectively. Adults dominated in both soil layers (Fig. 4; total catch: 84.3 and 75.1%, respectively). Subadults were more abundant in *A. dundoensis* (10.8%) compared to *A. proximus* (1.7%). *A. proximus* was more abundant in the organic soil layer (80.6%) compared to the mineral subsoil (Fig. 4: 3.5-7 cm). No males were obtained in *A. dundoensis*, and only two males each in *A. proximus* and *A. tenuis*.

Only in *Allopauropus proximus* was the monthly abundance of adults (250 females, 2 males) in both soil layers positively correlated with maximum soil temperatures (25.1-29.3 °C; average: 25.3 ± 0.7 °C), i.e. catch numbers increased with increasing temperatures (total catch: $r=+0.85055$ (0-3.5cm), $r=+0.81230$ (3.5-7cm), $p<0.01$; $n=12$). For all other species no significant correlations were obtained ($p \leq 0.01$) between the monthly abundances in the soil and the local abiotic factors.

Although the total catches of dominant species obtained during the dry season were generally higher compared to the rainy season, there was no distinct reproductive period because juveniles as well as adults occurred throughout the year (cf. Figs 5-7 for *Allopauropus rodriguesi*, *A. bicornutus*, *A. ovalis*, *A. manauensis*, *A. bicornulus* and *Hemipauropus piriformis*). These results indicate a plurivoltine mode of life.

DISCUSSION

Abundance and vertical distribution

Further comparable data on the abundance and vertical distribution of the soil fauna in four different upland forest types of Central Amazonia were obtained by Adis and collaborators (cf. Adis *et al.* 1987a,b, 1989a,b; Ribeiro 1994). Arthropods were collected to a soil depth of 14 cm during rainy and dry seasons and extracted with the Kempson method as described above. Between 75% and 92% of all arthropods were found to inhabit the top 7 cm when Acari and Collembola were included in the total catch numbers and 69%-84% when they were omitted. Data on Pauropoda are now available:

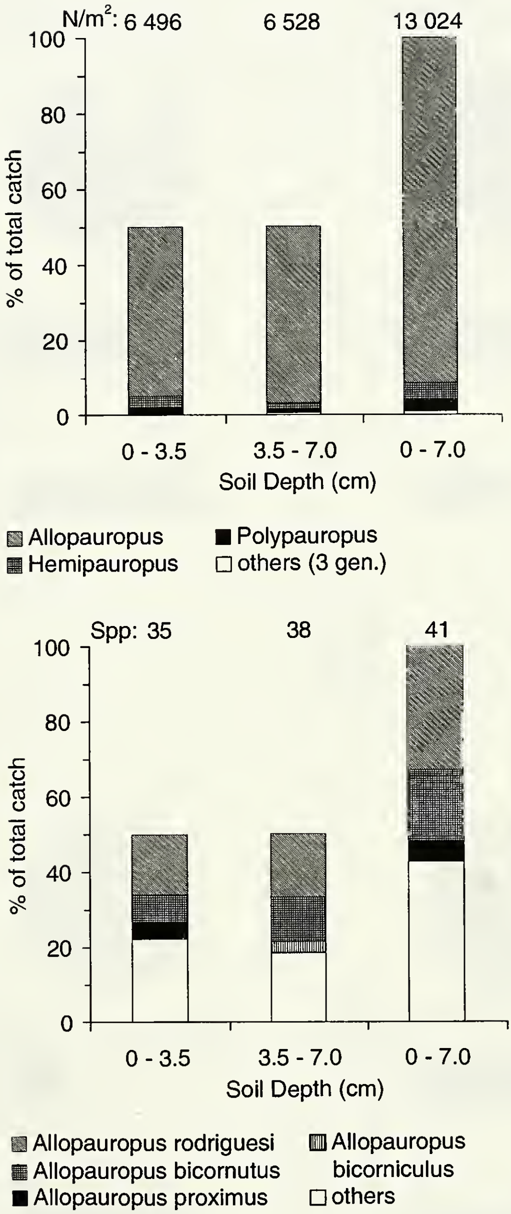

FIG. 3

Distribution of dominant genera (top) and species (bottom) of Pauropoda in the soil according to depth in a secondary upland forest near Manaus. (Total catch = 100%). Samples taken monthly at 0-3.5 and 3.5-7 cm depths between September 1982 and August 1983. (N = total number of specimens; Spp. = total number of species).

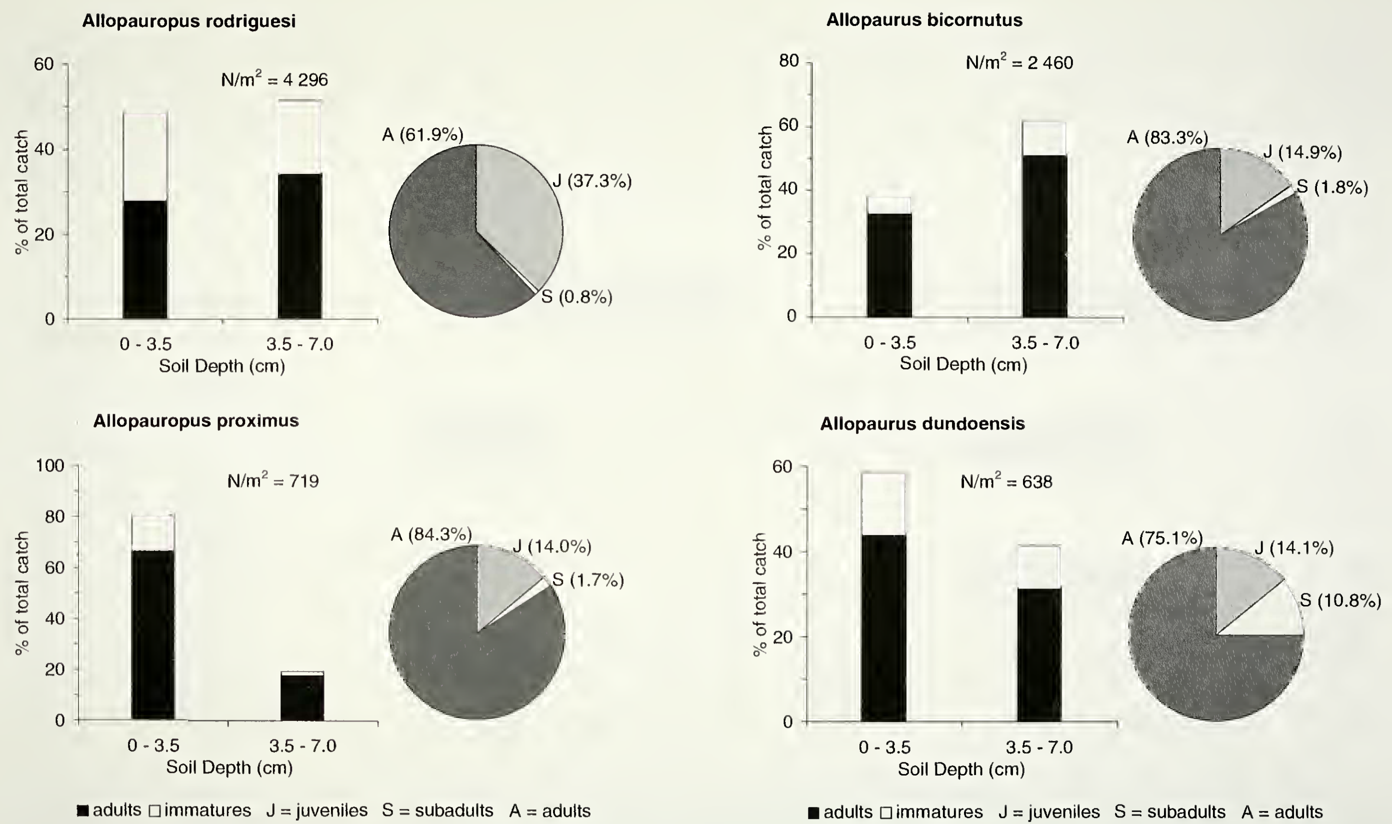

FIG. 4

Distribution of *Allopauropus rodriguesi*, *A. bicornutus*, *A. proximus* and *A. dundoensis* in the soil according to depth, and percentage of developmental stages in a secondary upland forest near Manaus. (Total catch = 100%). Samples taken monthly at 0-3.5 and 3.5-7 cm depths between September 1982 and August 1983. (N = total number of specimens).

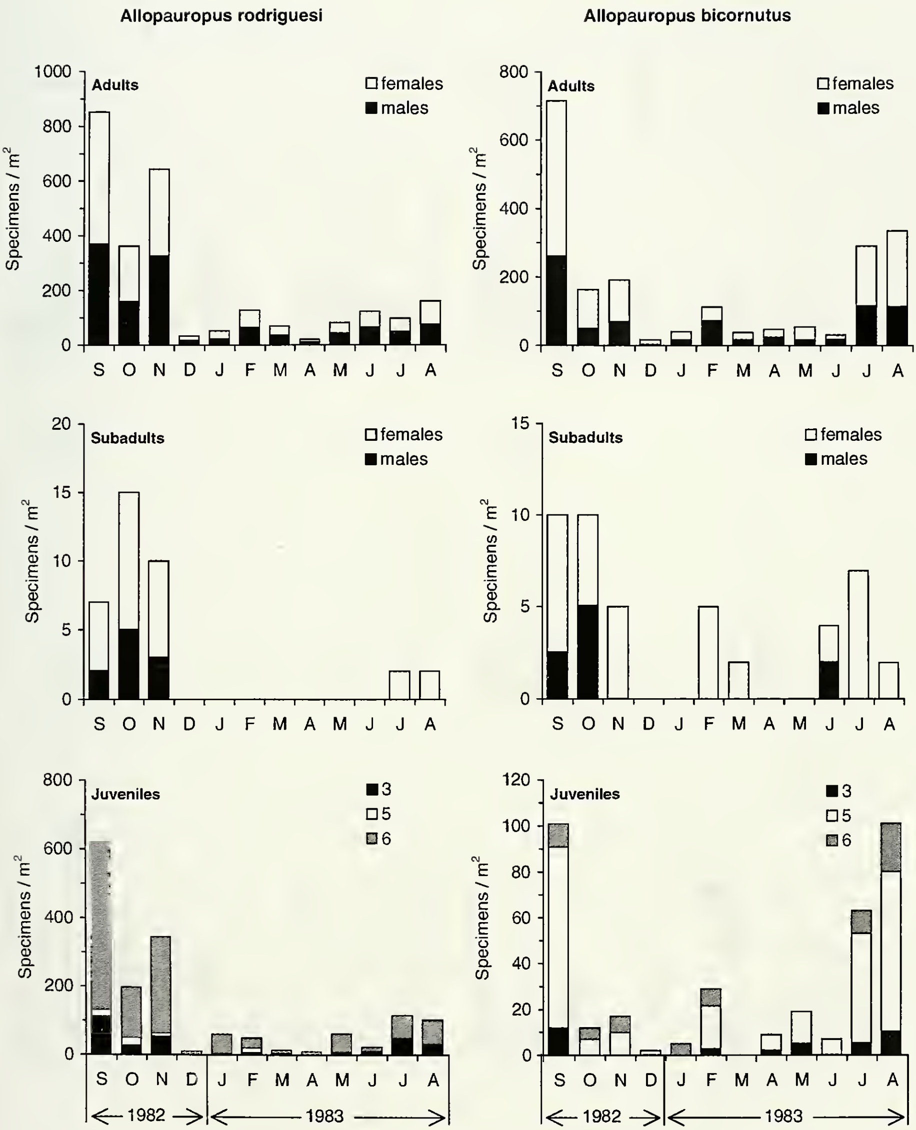

FIG. 5

Temporal occurrence of developmental stages of *Allopauropus rodriguesi* and *A. bicornutus* in the soil (N/m^2 in 0-7 cm depth) of a secondary upland forest near Manaus. Monthly samples taken between September 1982 and August 1983. (Classification of juveniles according to pairs of legs).

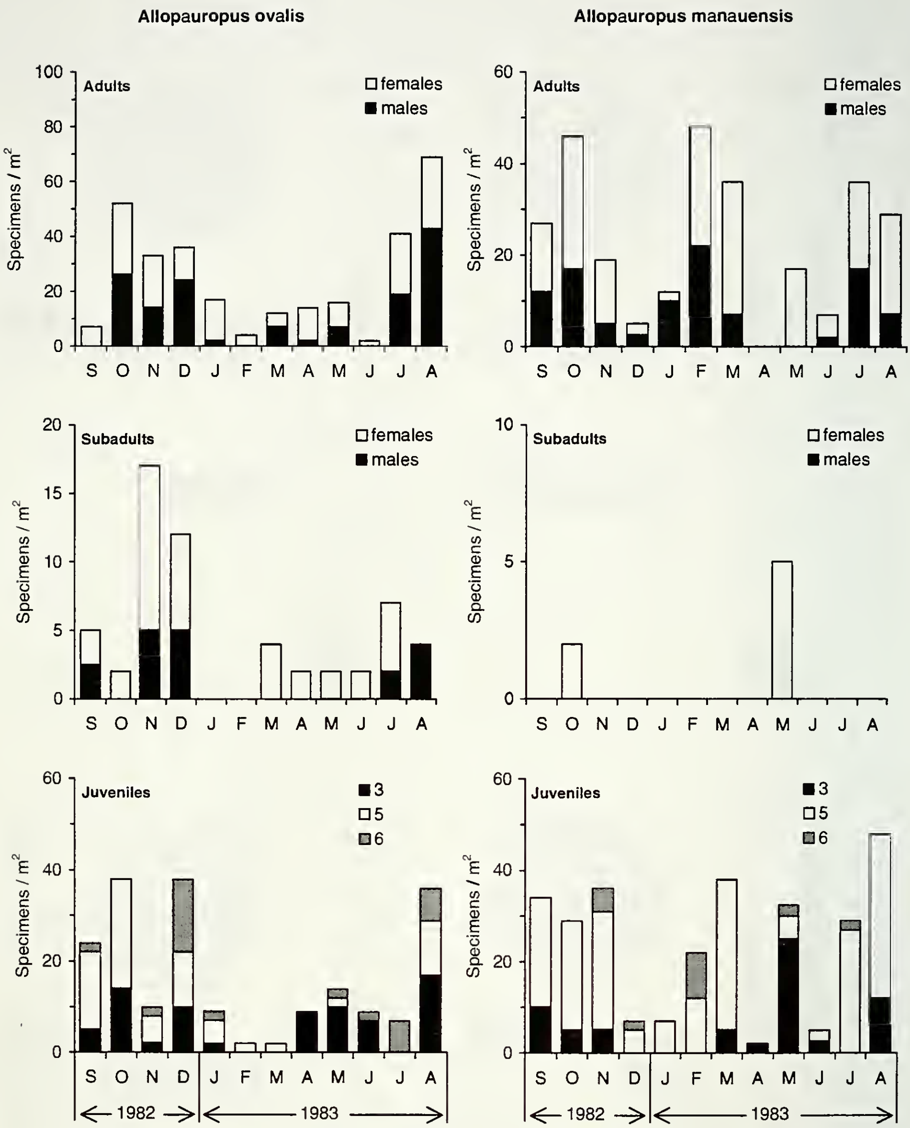

FIG. 6

Temporal occurrence of developmental stages of *Allopauropus ovalis* and *A. manauensis* in the soil (N/m^2 in 0-7 cm depth) of a secondary upland forest near Manaus. Monthly samples taken between September 1982 and August 1983. (Classification of juveniles according to pairs of legs).

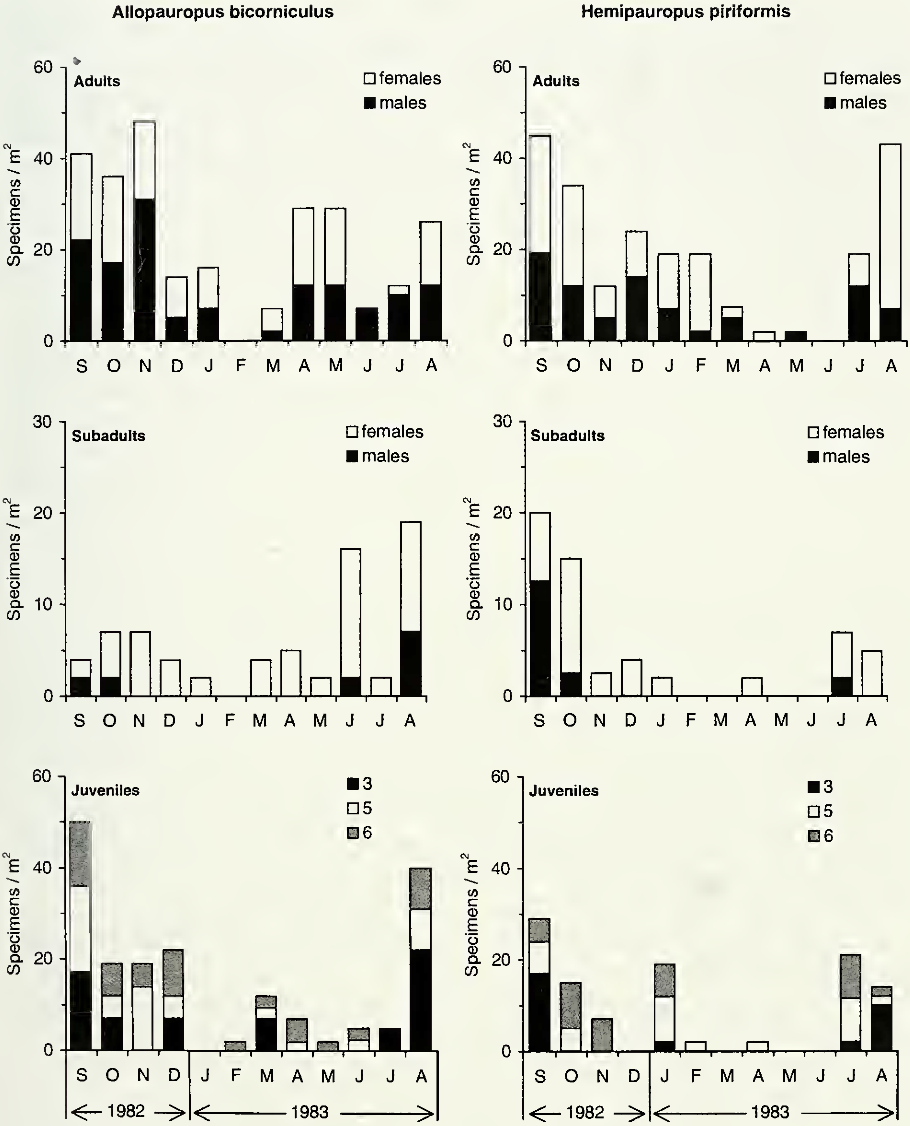

FIG. 7

Temporal occurrence of developmental stages of *Allopauropus bicorniculus* and *Hemipauropus piriformis* in the soil (N/m^2 in 0-7 cm depth) of a secondary upland forest near Manaus. Monthly samples taken between September 1982 and August 1983. (Classification of juveniles according to pairs of legs).

One study was conducted during October 1985 and April 1986 in a secondary upland forest on yellow latosol (Capoeira) at the INPA campus in Manaus (03°08'S, 60°01'W), where the vegetation was previously cut but unburned (ADIS *et al.* 1987a,b). Pauropods represented 1.1-1.6% of the total arthropods when Acari and Collembola were included (dry season: 50.448 ind./m^2, rainy season: 63.850 ind./m^2) and 4.6-5.8% when they were omitted from the total catch numbers (dry season: 11.934 ind./m^2, rainy season: 17.886 ind./m^2). The total abundance of pauropods in 0-14 cm soil depth was higher during the rainy season (1,035 ind/m^2) compared to the dry season (549 ind./m^2). However, during both rainy and dry seasons percentages of the total catch in the top 7 cm were similar (61.9% and 66.7%, respectively).

Another study was made from August 1990 to February 1991 in a secondary upland forest on yellow latosol (Capoeira), about 50 km north of Manaus (03°34'S, 60°60'W), where the vegetation was previously cut and burned (RIBEIRO 1994). Pauropods represented 2.5-3.5% of the total arthropods when Acari and Collembola were included (dry season (Aug.-Oct.): 29.064 ind./m^2, rainy season (Dec.-Febr.): 19.793 ind./m^2) and 9.4-9.8% when they were omitted from the total catch numbers (dry season: 7.720 ind./m^2, rainy season: 7.176 ind./m^2). The total abundance of pauropods (0-14 cm soil depth) during the rainy and dry seasons was similar (703 versus 727 ind./m^2). This was also true for the percentages obtained in the top 7 cm: 42.5% of the total catch during the rainy season and 55.0% during the dry season.

A third study was made during March and August 1988 in a primary forest on whitesand soil (Campinarana), about 45 km north of Manaus (02°35'S, 60°01'W; ADIS *et al.* 1989a,b). Pauropods represented 2.8-4.4% of the total arthropods when Acari and Collembola were included (dry season: 57.703 ind./m^2, rainy season: 74.255 ind./m^2) and 13.8-18.1% when they were omitted from the total catch numbers (dry season: 14.119 ind./m^2, rainy season: 15.023 ind./m^2). The total abundance of pauropods (0-14 cm soil depth) during the rainy and dry seasons was similar and high (2,079 versus 2,550 ind./m^2). This was also true for the percentages obtained in the top 7 cm: 60.4% of the total catch during the rainy season and 61.9% during the dry season.

The fourth study was conducted during April and October 1987 in the primary upland forest on yellow latosol at Reserva Ducke (ADIS *et al.*, unpubl.). Pauropods represented 1.3-1.7% of the total arthropods when Acari and Collembola were included (dry season: 38.727 ind./m^2, rainy season: 25.905 ind./m^2) and 4.1-4.3% when they were omitted from the total catch numbers (dry season: 11.742 ind./m^2, rainy season: 11.005 ind./m^2). The total abundance of pauropods (0-14 cm soil depth) during the rainy and dry seasons was similar and low (448 versus 505 ind./m^2). No significant difference (Chi-square test) was found between the percentages obtained in the top 7 cm during the rainy season (62.4% of the total catch) and the dry season (84.4%).

The lack of pauropods in samples from the ground and arboreal photo-eclector indicates that representatives of this group are rarely active on or above the soil surface in Central Amazonian upland forests. This conclusion is supported by two other studies in a primary upland forest of the Reserva Ducke near Manaus, in which apparently no pauropods were collected in 20 baited pitfall traps and in one or more ground photoeclectors during a sample period of 12 months (ADIS *et al.* 1996, PENNY & ARIAS 1982) or from tree crowns by fogging canopies with pyrethrum (ADIS *et al.* 1997c).

The depth to which pauropods occur in the soil of the Central Amazonian upland forests is unknown. Our studies in various forest types near Manaus (see above) revealed their presence to a soil depth of 14 cm. SERAFINO & MERINO (1978) detected them until 20 cm soil depth in a forest and in plantations in Costa Rica. Pauropoda are, however, found to occur to a depth of at least 75 cm in other parts of the world (SCHELLER 1974). In *Allopauropus proximus* the vertical distribution was influenced by soil temperatures. In the soil of man-made pastures (0-14 cm depth) adjacent to upland forests in Central Amazonia, pauropods were only found below 7 cm soil depth. One reason might be the low humidity and high temperature of the soil around noon, particularly during the dry season (ADIS & FRANKLIN, unpubl.).

The small size of pauropods as well as inefficient sampling methods might explain their "absence" or low abundances in other studies on the Neotropical arthropod fauna in 0-30 cm soil depth (e.g. HARADA & BANDEIRA 1994a,b; HÜTHER 1985; MACAMBIRA 1997).

PARTHENOGENESIS

Two pauropod species of this study had strikingly low sex ratios: *Allopauropus proximus* (2 males and 250 females; sex ratio 0.008) as well as *A. tenuis* (2 males and 211 females; sex ratio 0.009). *A. dundoensis* is only known from 200 females from the secondary upland forest under study. The two first mentioned species have often been reported from tropical and subtropical areas. Although hundreds of specimens were sexed, no males at all were found in *A. proximus* and a few ones only in *A. tenuis* (SCHELLER 1970). *A. dundoensis* has not often been collected outside Amazonia. It was previously known from about the same latitude in tropical West Africa only (REMY 1955, 1956; SCHELLER 1975) from where 29 specimens were sexed, 28 of them females and 1 male. The latter specimen was subadult and somewhat deviated from the type material. Even if it should belong to *A. dundoensis*, males seem to be extremely rare. In conclusion, males in *A. proximus* and *A. tenuis* seem to be very rare and in *A. dundoensis* they may not exist at all. As far as known *A. proximus* is parthenogenetic, *A. tenuis* probably so, at least in parts of its range, and *A. dundoensis* might be.

In two studies of north African pauropods, REMY (1947) established a striking scarcity of males in two *Allopauropus* species. In most of the European countries where he had found *Allopauropus vulgaris* (Hansen) the sex ratio was about 1.0 but in an Algerian material (99 specimens sexed adult and subadults) he could not find males at all (REMY 1947). He found a similar situation in *A. productus* Silvestri: from Europe, he reported 54 males and 70 females (sex ratio 0.77); in Algerian and Tunisian material with 155 sexed adults and subadults, there were 54 males and 101 females (sex ratio 0.53); from Morocco only 4 specimens among 73 adults and subadults were males (sex ratio 0.05) (REMY 1952). Similar sex ratios have later also been found in these species (material from Corsica: LECLERC 1953; from the Canary Islands: SCHELLER 1979) but also in other species e.g. in *A. gracilis* (Hansen) from Canada (sex ratio 0.32)

(SCHELLER 1984) as well as in *A. cuenoti* (Remy) from Switzerland (sex ratio 0.07) (SCHELLER 1976) and the Canary Islands with no males at all (SCHELLER 1979). It seems evident that populations with both males and females as well as pure female populations exist in the Pauropoda. Since in millipedes males are much rarer than females and in some species both bisexual and thelytokous forms appear (ENGHOFF 1978), probably due to the presence of bacteria (ADIS *et al.* 1999), it is plausible that the same types of reproduction have arisen in the Pauropoda too.

The sex ratio is generally low in the Pauropoda and there may be a decrease of sexual reproduction in some species (SCHELLER 1970). In many species from all parts of the world males are unknown, but in most cases the numbers of adult and subadult specimens recorded are too low to decide whether they are parthenogenetic or not. Up to now, no laboratory studies have been performed to show parthenogenesis in the Pauropoda.

Besides spanandry there is one more factor indicating the occurrence of parthenogenetic reproduction in some species. The genus *Allopauropus* has two subgenera, the nominate subgenus with 3 pairs of setae on the pygidial sternum and 9 pairs of legs in the adult stage, and *Decapauropus* with 2 pairs of setae on the pygidial sternum and two adult stages, one with 9 pairs of legs and an additional one with 10 pairs of legs. All the specimens of the latter stage, which have been sexed, have been females and this stage seems to be more frequent in areas with an unfavourable environment than in areas with moist and not too cold climates. It might be an adaptation to a parthenogenetic form of reproduction, occurring in areas with in some way harsh climates. Under good environmental conditions in the tropics the additional stage with 10 pairs of legs is very rare, Amazonia included.

The development of spanandry or even a thelytokous reproduction in *Allopauropus* seems to have arisen particularly in the subgenus *Decapauropus*. It is noteworthy, however, that in the material from the secondary upland forest near Manaus, a species in *Allopauropus* s. str., *A. (A.) dundoensis*, seems to have such a low sex ratio that parthenogenetic reproduction might be conceivable.

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